Naive Juveniles Are More Likely to Become Breeders after Witnessing Predator Mobbing

Griesser, Michael ; Suzuki, Toshitaka N

DOI: https://doi.org/10.1086/689477

Naïve juveniles are more likely to become breeders after witnessing predator mobbing

Michael Griesser [1,2,*], Toshitaka Suzuki 3,4,†

1 Department of Anthropology, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

2 Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Krakow, Poland

3 Department of Evolutionary Studies of Biosystems, SOKENDAI (The Graduate University for Advances Studies), Hayama, 240-0193 Kanagawa, Japan

4 Center for Ecological Research, Kyoto University, 2 Hirano, Otsu, Shiga 520-2113, Japan

* Corresponding author: michael.griesser@uzh.ch

ORCID Griesser: http://orcid.org/0000-0002-2220-2637

ORCID Suzuki: http://orcid.org/0000-0001-6405-7653

Short title: The consequences of witnessing mobbing

Abstract

Responding appropriately during the first predatory attack in life is often critical for survival. In many social species, naïve juveniles acquire this skill from conspecifics, but its fitness consequences remain virtually unknown. Here we experimentally demonstrate how naïve juvenile Siberian jays (*Perisoreus infaustus*) derive a long-term fitness benefit from witnessing knowledgeable adults mobbing their principal predator, the goshawk (*Accipiter gentilis*). Siberian jays live in family groups of 2-6 individuals that also can include unrelated non-breeders. Field observations showed that Siberian jays only rarely encounter predators and indeed, naïve juveniles do not respond to predator models when on their own, but do when observing other individuals mobbing them. Predator exposure experiments demonstrated that naïve juveniles had a substantially higher first-winter survival after observing knowledgeable group members mobbing a goshawk model, increasing their likelihood of acquiring a breeding position later in life. Previous research showed that naïve individuals may learn from others how to respond to predators, care for offspring or choose mates, generally assuming that social learning has long-term fitness consequences without empirical evidence. Our results demonstrate a long-term fitness benefit of vertical social learning for naïve individuals in the wild, emphasizing its evolutionary importance in animals, including humans.

Keywords:

Survival, predation risk, mobbing behavior, antipredator behaviors, prey response, teaching

Introduction

Responding appropriately during predator encounters is a vital skill for animals, and it is critical to respond appropriately already during the first predator attack in life. Animals have evolved different mechanisms to display appropriate anti-predator responses (Caro 2005; Griffin 2004; Hollén and Radford 2009; Wisenden 2003). Some species have innate predator recognition where individuals exhibit appropriate antipredator behaviors already during the first predator encounter in life (Curio 1993; Li 2002; Storm and Lima 2010). Innate predator recognition is especially beneficial when trial-and-error learning is fatal, in solitary species or in social species where naïve juveniles do not have the opportunity to learn from knowledgeable individuals (Hollén and Radford 2009; Li 2002; Suzuki 2016). In contrast, individuals in many social species learn to respond appropriately to predators from other individuals (Caro 2005; Hollén and Radford 2009), or modify existing templates depending on the response of knowledgeable individuals (Cheney and Seyfarth 1980). Learned predator recognition is advantageous when species face a variety of risk of predation that can change in a short-time scale (Wisenden 2003).

Naïve individuals can learn to recognize predators using chemical cues (i.e., the odor of injured conspecifics; Wisenden 2003), or when observing knowledgeable individuals interacting with predators, for example during predator mobbing (Curio et al. 1978; Graw and Manser 2007; Reader and Biro 2010). Non-hunting predators pose a low immediate risk to prey, and many species approach and mob them (Caro 2005; Dugatkin and Godin 1992; Flasskamp 1994). Laboratory experiments showed that individuals quickly learn to respond to novel predators when observing others mobbing them (Curio et al. 1978; Manassa and McCormick 2013), which can improve their short-term survival (i.e., 2-3 days subsequent to the predator exposure; Lönnstedt et al. 2012; Manassa and McCormick 2013). Yet, virtually no field study has investigated the long-

term fitness consequences of naïve individuals observing knowledgeable individuals mobbing predators (but see Shier and Owings 2007).

Here we report on field experiments in Siberian jays (*Perisoreus infaustus*) to test the effect of a single exposure to a predator model early in life on subsequent survival and the probability to become a breeder. This sedentary bird species lives in stable family groups of 2-6 individuals that are formed through the retention of offspring from different cohorts for up to 5 years (i.e., retained offspring), and/or the immigration of unrelated non-breeders (i.e., immigrants) mostly during the first summer of their life (Ekman and Griesser 2016; Griesser et al. 2014). Within successful broods, dominant siblings evict subordinate brood mates from the parental territory in July, about 1-2 months after fledging (fig. 1). These juveniles (i.e., individuals during their first year of life) disperse and settle usually within less than 2 days after leaving the parental territory in another group as immigrant group member (Ekman et al. 2002).

The agents of mortality are well known in our study population. Hawks (goshawk *Accipiter gentilis,* sparrowhawk *A. nisus*) account for 70% of all deaths, large owls (hawk owl *Surnia ulula*, Ural owl *Strix uralensis*) account for 25% of all deaths, while the remaining 5% are killed by European pine marten (*Martes martes*) (Griesser 2013; Griesser et al. 2006). However, Siberian jays rarely encounter predators between fledgling in the end of May and the time the experiments were finished early October (fig 1). During the three years of this study, very few owls were present at the study site, and thus, the estimated encounter rates of owls for a group between end of May and early October ranged from 0 to 0.06, while encounter rates for goshawks ranged from 0.02 to 0.42 and for sparrowhawks from 0.02 to 0.80. Most encounters with goshawks and sparrowhawks involved hawks passing by at distance (> 30 m away), while

8% of hawk encounters were attacks or close encounter with Siberian jays (< 30 m), and only 3% of all hawk encounters resulted in mobbing. These observations suggest that juveniles have almost no opportunity to observe the behavior of knowledgeable individuals during predator encounters.

Indeed, juveniles approach a feeder to forage near perched predator models when encountering them on their own, but do immediately copy the mobbing behavior of knowledgeable group members when exposed together (Griesser and Ekman 2005; Griesser and Suzuki 2016). Upon discovering a perched live predator or a perched taxidermized predator model, group members immediately start to approach the predator by moving from tree to tree, swoop over it and give mobbing calls for several minutes (Griesser and Ekman 2005). Usually all group members participate in mobbing but male breeders give most mobbing calls. Groups mob more dangerous predators (hawks) longer than less dangerous predators (owls), particularly in the presence of retained offspring (Griesser 2009; Griesser and Ekman 2005; Griesser and Suzuki 2016).

Earlier studies have shown that older individuals have a lower mortality than juveniles, which suggests that juveniles lack anti-predator skills (Griesser et al. 2006). They also showed that retained juveniles have lower mortality than immigrant juveniles (Ekman and Griesser 2016; Griesser et al. 2006). This difference may reflect that breeders provide retained offspring with nepotistic predator protection (Griesser and Ekman 2004; Griesser and Ekman 2005), or that retained juveniles, being in closer association with their parents (Griesser et al. 2006), have more opportunities to observe knowledgeable individuals interacting with predators than immigrant juveniles (Griesser and Suzuki 2016). When encountering a perched predator, retained juveniles

follow their parents closely during mobbing and when leaving, while immigrant juveniles mob more independently and often leave on their own (Griesser and Suzuki 2016).

Based on these earlier findings, we hypothesize that naïve juveniles have an improved first-winter survival after observing knowledgeable individuals mobbing a predator in autumn, and thus, are more likely to become breeder. If acquired predator recognition is species-specific, only juveniles that are exposed to a goshawk (the main predator species present at the study site during winter; fig. 1) will experience a higher first winter survival. Juveniles exposed to a sparrowhawk may experience higher survival after their first winter of life, between April and September, when sparrowhawks are present at the study site (fig. 1). If jays learn to recognize predator categories, such as hawks and owls, juveniles exposed to either a goshawk or a sparrowhawk (sparrowhawks resemble goshawks but are smaller) will experience a higher first winter survival than those exposed to owls. If naïve juveniles generally benefit from observing knowledgeable individuals mobbing predators, all juveniles observing any predator mobbing are predicted to have a higher winter survival. In addition, retained juveniles are predicted to have a higher first winter survival than immigrant juveniles given the nepotistic antipredator protection from their parents (Griesser 2003; Griesser and Ekman 2005). We tested these hypotheses by placing models of different predators (goshawk, sparrowhawk, hawk owl, Ural owl) near a feeder in 43 groups during autumn and monitored the subsequent winter survival and breeding status of the juveniles (table A1). We compared the influence of exposure to different combinations of predator models or a control situation (no experimental mobbing; table A1).

Methods

This study was conducted in a color-ringed population of Siberian jays that has been studied from 1989 onwards near Arvidsjaur, northern Sweden (Griesser and Lagerberg 2012). Here, we use experimental data collected between autumn 1999 and autumn 2003, and individual life-history data collected up to autumn 2006. Aside from a few exceptions ($N = 3$), all birds in the study population were individually color-ringed. Blood (50 µl) was taken from all individuals for molecular sex and kinship determination (Griesser et al. 2015; Griffiths et al. 1998). Experiments were performed under the license of Umeå djurförsöksetiska nämd (license number A80-99 and A45-04).

Predator experiments

We presented 43 Siberian jay groups (containing 109 juveniles) with combinations of different taxidermized predators mounted in upright perched posture or no predator model between late August and early October years 1999-2000 and 2003 (fig. 1; table A1). In 1999 and 2000, we exposed groups to a sparrowhawk and/or an Ural owl model in randomized order. In 2003, we exposed groups to a hawk owl and/or a goshawk model, randomly assigning treatment type to groups; however, experiments with the goshawk model always took place after exposure to the hawk owl model due to constraints in model availability. We excluded in this study experiments done in groups that did not include juveniles. We only used one taxidermized model of each species, but the response of jays to the models closely matched their response to live perched predators (Griesser 2008; Griesser 2009; Griesser and Suzuki 2016), suggesting that the models were representative for the respective species.

For each trial, a model was positioned 5 m away from a feeder on a 1 m high pole, and concealed with a plastic cover before the jays were attracted to the feeder by whistling. Once group

members had foraged undisturbed for 15 minutes the model was exposed. Breeders were usually the first individuals to detect the model and initiate mobbing (Griesser and Ekman 2005; Griesser and Suzuki 2016). After the whole group had stopped mobbing and had moved more than 50 m away from the predator model, we covered the model again. For each experiment in the same group, the feeder and the model were placed in a different location near the center of the territory.

We randomly selected control groups that were not exposed to any predator model during the same years (N = 56 juveniles in N = 27 groups; N = 2 juveniles in 1999, N = 21 juveniles in 2000, N = 33 juveniles in 2003). We repeatedly visited these groups to record the group composition. Juveniles that advanced into a breeder position before March were excluded from the analyses (N = 4), given that rank influences survival (Ekman and Griesser 2016; Griesser et al. 2006). We also excluded N = 23 juveniles that were exposed to an attacking goshawk model (Griesser 2013) as this could provide juveniles with the knowledge of how to react during an attack and not only provide an opportunity to learn to recognize a goshawk as a predator.

Survival assessment

To assess the survival of juveniles subsequent to the experiments, we visited all groups at least twice in early March the following year, before the onset of the breeding season and the dispersal of juveniles into breeding openings, and recorded all birds present (fig. 1). Earlier studies showed that this method reliably assesses overwinter survival in the Siberian jay. The remains of all radio-tagged individuals that disappeared during winter (i.e., large feathers, bones, legs) were retrieved on their territory, and all these individuals were depredated by predators (Griesser 2013; Griesser et al. 2006). Since jays rely on numerous individually stored food items to survive

winter, dispersing off the territory during winter would be maladaptive as such individuals would be likely to starve.

Acquisition of breeding position

We used data on individual life-histories to assess whether juveniles that were included in the study subsequently acquired a breeding position. We visited all groups at least twice in March before the breeding season, and in September after emigration and immigration of juveniles during all years, and noted the presence of all individuals. Up to 2004, the social rank of individuals was known since the breeding attempts of all groups included in this study were followed (Griesser et al. 2014). In 2005 and 2006, breeding attempts were not followed, and thus we assessed the social rank of group members using the behavior of individuals foraging on feeders placed in the territory (Griesser et al. 2014). This assessment was conducted following a standardized protocol (Ekman et al. 1994) to ascertain the social rank of all group members. Breeders are dominant over other group members (Ekman and Sklepkovych 1994), and are tolerant towards their own offspring on feeders, whereas they aggressively chase unrelated group members from the feeder (Griesser 2003; Griesser et al. 2015). We followed all juveniles included in the study until they either were dead (or had emigrated from the study population), or were still alive as a breeder at the end of the sampling period. Given that juveniles that disappeared after the first winter could have either been killed or emigrated from the study population, this method is a conservative measure. It is reasonable to assume that the likelihood of experimental individuals dispersing outside of the study population was independent of their exposure to predator models.

Assessment of kinship, age of non-breeders, and habitat structure

In Siberian jays, the survival of juveniles is influenced by kinship and habitat structure of the territory (Griesser et al. 2006), and thus, we included these factors in the statistical analyses described below. We assessed the kinship of juveniles using three methods. In most groups the reproductive success was monitored by locating nests and ringing all nestlings in successful broods (N=82 broods; Ekman et al. 2001; Griesser et al. 2008). Alternatively, juveniles were caught 1-4 weeks after they had fledged but could still be ringed before dispersal (N = 8 broods). In groups where reproduction had not been followed (N = 4 broods), the relatedness of unringed juveniles was determined using molecular methods (Griesser et al. 2015). The age of individuals was assessed by using the known birth year. Unringed juveniles can be reliably aged using the shape of the outermost tail feather (Svensson 2006).

Forests at the study site cover a gradient from intensely managed to pristine patches (Griesser et al. 2007). In managed patches, the entire understory is removed every 20-40 years to enhance timber production (Griesser et al. 2007). These patches are more open and provide less visual cover than unmanaged patches, facilitating prey detection for predators (Griesser and Nystrand 2009). We measured the proportion of unmanaged patches that had not been affected by forestry for at least 50 years within each territory in the field with a GPS receiver or from aerial images.

Statistical analyses

Since all juveniles exposed to a goshawk model survived, it was not possible to analyze these data with likelihood-based statistics, and thus we used binomial models in the MCMCglmm package (Hadfield 2010) in R 3.2.5 (R Core Team 2016). We used the default prior for binomial models, and used a burn-in of 50’000 iterations, a thinning interval of 500 and a total of 550’000 iterations to achieve model convergence, a low autocorrelation and balanced trace-plots. We ran

two sets of models to assess the influence of exposure to the different predator models on (i) first winter survival and (ii) the probability to become a breeder later on in life. Our models included the predator models an individual was exposed to (goshawk: yes, no, sparrowhawk: yes, no, hawk owl: yes, no, Ural owl: yes, no), sex, kinship, the total number of predator models an individual was exposed to, group size and the proportion of unmanaged forest on a territory as independent effects in the model. We included group identity as random effect in the models to control for repeated data sampling on territories, and year as random effect to control for the differences in the design between years and between-year differences in baseline mortality.

We ran an additional set of models to confirm that the differences in the experimental design did not influence our conclusions. Since groups that were exposed to both the hawk owl model and the goshawk model always were first exposed to the hawk owl, it was not possible to include the order of experimental exposure to the predator models and whether an individuals was exposed to a goshawk simultaneously into the analyses. To confirm that the order of exposure did not affect our conclusions, we re-ran both models specifying the last model the birds were exposed to. These models show that the order of exposure did not affect our conclusions (table A2).

Results

Exposure to specific predator species influenced the subsequent survival of juveniles. All 24 juveniles that had been exposed to a perched goshawk model survived their first winter of life, while 19-38% of juveniles that had been exposed to a sparrowhawk model, an owl model or no predator model disappeared ($P = 0.009$; fig. 2; table 1). Also, juveniles in smaller groups had a higher survival than juveniles in larger groups ($P = 0.013$; table 1). No other factor was found to influence the winter survival of juveniles. Moreover, juveniles that were exposed to a goshawk or

a sparrowhawk model had a higher probability of acquiring a breeding position, 0.5-3 years after the experiments compared to other juveniles (goshawk: $P = 0.015$; sparrowhawk: $P = 0.048$; fig. 2, table 1).

Discussion

Our results show that observing conspecifics mobbing the principal predator (goshawk) eliminates all first winter mortality of juvenile Siberian jays, boosting their chance of becoming a breeder. Since Siberian jays rarely encounter natural predators, most juveniles almost certainly had never observed knowledgeable individuals interacting with a live predator before our experiments. Therefore, a single exposure to knowledgeable individuals mobbing a goshawk model provided juveniles with the opportunity to learn to recognize the danger posed by goshawks, allowing them to respond appropriately in subsequent predator encounters. Exposure to a sparrowhawk model did not improve first winter survival when sparrowhawks are not present at the study site, yet it improved survival after their first winter of life, when jays could encounter these predators. Thus, juveniles learned to recognize specific predator species, despite the similar appearance of goshawks and sparrowhawks, suggesting that early exposure to potential predators facilitates their long-term recognition.

Alternative interpretations are not plausible in this case. First, it is unlikely that our experiments influenced the behavior of natural predators, as we never observed predators during our experiments. Second, improved juvenile survival could reflect improved protection by other group members during natural hawk encounters. Breeders increase their vigilance directly after exposure to a hawk or owl model (Griesser and Nystrand 2009), and invest more in vigilance,

mobbing behavior and warning calls when together with retained offspring (Griesser 2003; Griesser 2009; Griesser and Ekman 2004; Griesser and Ekman 2005). However, both immigrant and retained juveniles had a higher survival, suggesting that juveniles benefit more from recognizing the risk themselves than from protection provided by other group members (Griesser 2013).

Juveniles in larger groups had a lower first winter survival than juveniles in smaller groups. In larger groups, juveniles are exposed to aggression from both breeders and older non-breeders (Ekman and Sklepkovych 1994; Nystrand 2006). Consequently, subordinate individuals forage in more open micro-habitats (Nystrand 2006), increasing their risk of being killed by a goshawk. Alternatively, goshawks may detect larger groups more easily (Cresswell and Quinn 2011; Kenward 1978), increasing the mortality of inexperienced juveniles. Independent of the mechanism that increases mortality in larger groups, all juveniles that could observe knowledgeable individuals mobbing a goshawk model survived their first winter of life.

A wide range of animals learn to recognize predators from others, either indirectly through chemical cues of wounded individuals (Wisenden 2003; Wisenden and Millard 2001), or directly by observing experienced individuals interacting with predators (Curio et al. 1978; Griffin et al. 2000; Lönnstedt et al. 2012), and both mechanisms may involve learning from conspecifics or heterospecifics (Curio et al. 1978; Magrath et al. 2015; Wisenden 2003). Previous studies showed that learning to recognize predators provides short-term survival benefits. For example, juvenile coral reef damselfish *Pomacentrus wardi* exposure to predator cues in the lab have increased survival during the first 3 days after release in the wild (Lönnstedt et al. 2012). Exposing the same species to predator cues together with knowledgeable conspecifics improves short-term

survival in the lab (Manassa and McCormick 2013). Similarly, exposing captive reared juvenile black-tailed prairie dogs *Cynomys ludovicianus* together with knowledgeable individuals to predator models improved their survival after release in the wild (Shier and Owings 2007). Our results extend these previous findings by demonstrating that socially acquired predator recognition as long-term fitness consequences in Siberian jays. Observing experienced group members mobbing the primary predator eliminates all subsequent overwinter mortality of juveniles, thereby boosting their chance of becoming a breeder later in life.

The benefits of the early acquisition of predator-recognition skills are high and social learning can be a crucial help in acquiring this skill. Previous research showed that young individuals can learn from others how to respond to predators (Curio et al. 1978; Lönnstedt et al. 2012), care for offspring (Smith 2009) or how to choose mates (Freeberg 2000). However, almost all studies that have investigated social learning have assumed that it has long-term fitness consequences without empirical evidence (Hoppitt and Laland 2008; van Schaik 2010). Our results demonstrate a long-term fitness benefit of social learning for naïve individuals, and thus its adaptive significance. In a virtual setting, learning mainly from others has shown to be a winning strategy (Rendell et al. 2010), supporting the evolutionary importance of social learning (Boyd and Richerson 1985; van Schaik 2010). While social learning brings the risk of learning false or outdated information (Boyd and Richerson 1985; Danchin et al. 2004; Griffin 2004), in situations where other individuals are a reliable source of information, such as during predator encounters where knowledgeable individuals benefit from responding appropriately, reliable information can spread between individuals. More generally, in particular parents are interested to provide their offspring with reliable learning opportunities (Griesser and Suzuki 2016). Prolonged parent-offspring association (Drobniak et al. 2015) increases the opportunities for offspring to acquire

life-skills by both providing a safe haven that allows for individual learning, increased opportunities for social learning and teaching (Griesser and Suzuki 2016), setting the stage for culture as the case in our own species (van Schaik 2010).

Acknowledgements

We dedicate this study to the late Jan Ekman who recently passed away, too early. We thank Folke and Maj Lindgren for sharing their knowledge of the jays, and Jan Ekman, Vittorio Baglione and Kara Belinsky for help in the field. The journal club of the Anthropological Institute, Judith Burkart, Simone Webber and Carel van Schaik gave helpful comments on the manuscript, and Szymek Drobniak gave statistical advice. This study was supported by the Swiss National Science Foundation (grant number PPOOP3_123520 to MG) and the National Science Centre, Poland, through the European Union's Horizon 2020 research and innovation programme (Marie Sklodowska-Curie grant No. 665778 to MG).

Table A1. Overview of the number of retained juveniles (kin) and immigrant juveniles (non-kin) as well as the number of groups exposed to different combinations of perched predator models. The total number of groups ($N = 43$) is smaller than the sum over all groups ($N = 65$) as groups that were exposed in different years to different predators are here listed as different group.

predator model	kin	non-kin	groups
goshawk	0	4	2
goshawk, hawk owl	11	9	12
hawk owl	3	2	4
sparrowhawk	3	2	3
sparrowhawk, Ural owl	2	9	11
Ural owl	5	3	6
no predator model	18	38	27
total *N*	42	67	43

Table A2. Effect of predator exposures during autumn on winter survival and the subsequent acquisition of a breeding position in Siberian jays, depending on the last predator model seen (goshawk: $N = 24$, sparrowhawk: $N = 10$, Ural owl: $N = 14$, hawk owl: $N = 5$, no predator model seen: $N = 56$). Data were analyzed using the MCMCglmm package (binomial distribution).

i) first winter survival

Factor	Posterior mean	Upper to lower CI	Effective sampling	*P* MCMC
intercept	1.13	0.73 to 1.57	1094	0.0009
goshawk	**0.36**	**0.15 to 0.61**	**1194**	**0.004**
hawk owl	-0.11	-0.49 to 0.3	1094	0.58
sparrowhawk	0.17	-0.12 to 0.45	1094	0.26
Ural owl	0.02	-0.22 to 0.25	1094	0.86
kinship: unrelated immigrants	0.04	-0.12 to 0.2	1094	0.64
sex: male	0.09	-0.06 to 0.27	1094	0.25
group size	**-0.13**	**-0.21 to -0.02**	**1094**	**0.013**
habitat structure	0.05	-0.19 to 0.29	1094	0.68

ii) becoming a breeder

Factor	Posterior mean	Upper to lower CI	Effective sampling	*P* MCMC
intercept	0.14	-0.35 to 0.61	1094	0.59
goshawk	**0.28**	**0.03 to 0.56**	**1094**	**0.04**
hawk owl	-0.23	-0.67 to 0.17	1094	0.31
sparrowhawk	**0.31**	**0.01 to 0.61**	**1275**	**0.05**
Ural owl	-0.03	-0.29 to 0.25	1094	0.84
kinship: unrelated immigrants	**0.19**	**0.01 to 0.37**	**1634**	**0.04**
sex: male	0.16	-0.02 to 0.33	1094	0.09
group size	-0.02	-0.13 to 0.09	1094	0.74
habitat structure	-0.01	-0.28 to 0.24	1002	0.94

References

Boyd, R., and P. Richerson. 1985. Culture and the Evolutionary Process. Chicago: Univ. Press, Chicago.

Caro, T. 2005, Antipredator defenses in birds and mammals. Chicago, Chicago University Press.

Cheney, D. L., and R. M. Seyfarth. 1980. Vocal recognition in free-ranging vervet monkeys. Animal Behaviour 28:362-367.

Cresswell, W., and J. L. Quinn. 2011. Predicting the optimal prey group size from predator hunting behaviour. Journal of Animal Ecology 80:310-319.

Curio, E. 1993. Proximate and developmental aspects of antipredator behavior. Advances in the Study of Behavior 22:135-238.

Curio, E., U. Ernst, and W. Vieth. 1978. Cultural Transmission of Enemy Recognition: One Function of Mobbing. Science 202:899-901.

Danchin, É., L.-A. Giraldeau, T. J. Valone, and R. H. Wagner. 2004. Public information: from nosy neighbors to cultural evolution. Science 305:487-491.

Drobniak, S. M., G. Wagner, E. Mourocq, and M. Griesser. 2015. Family living: an overlooked but pivotal social system to understand the evolution of cooperative breeding. Behavioral Ecology 26:805-811.

Dugatkin, L. A., and J. G. J. Godin. 1992. Prey Approaching Predators - a Cost-Benefit Perspective. Annales Zoologici Fennici 29:233-252.

Ekman, J., S. Eggers, and M. Griesser. 2002. Fighting to stay: the role of sibling rivalry for delayed dispersal. Animal Behaviour 64:453-459.

Ekman, J., S. Eggers, M. Griesser, and H. Tegelström. 2001. Queuing for preferred territories: delayed dispersal of Siberian jays. Journal of Animal Ecology 70:317-324.

Ekman, J., and M. Griesser. 2016. Siberian jays: delayed dispersal in absence of cooperative breeding, Pages 6-18 *in* W. D. Koenig, and J. Dickinson, eds. Cooperative Breeding in Vertebrates: Studies of Ecology, Evolution, and Behavior. Cambridge, Cambridge University Press.

Ekman, J., and B. Sklepkovych. 1994. Conflict of interest between the sexes in Siberian jay winter flocks. Animal Behaviour 48:485.

Ekman, J., B. Sklepkovych, and H. Tegelström. 1994. Offspring retention in the Siberian jay (Perisoreus infaustus) - The prolonged brood care hypothesis. Behavioral Ecology 5:245-253.

Flasskamp, A. 1994. The Adaptive Significance of Avian Mobbing .5. an Experimental Test of the Move on Hypothesis. Ethology 96:322-333.

Freeberg, T. M. 2000. Culture and courtship in vertebrates: a review of social learning and transmission of courtship systems and mating patterns. Behavioural Processes 51:177-192.

Graw, B., and M. B. Manser. 2007. The function of mobbing in cooperative meerkats. Animal Behaviour 74:507-517.

Griesser, M. 2003. Nepotistic vigilance behavior in Siberian jay parents. Behavioral Ecology 14:246-250.

—. 2008. Referential calls signal predator behavior in a group-living bird species. Current Biology 18:69-73.

—. 2009. Mobbing calls signal predator category in a kin group-living bird species. Proceedings of the Royal Society B-Biological Sciences 276:2887-2892.

—. 2013. Do warning calls boost survival of signal recipients? Evidence from a field experiment in a group-living bird species. Frontiers in Zoology 10:49.
Griesser, M., and J. Ekman. 2004. Nepotistic alarm calling in the Siberian jay, Perisoreus infaustus. Animal Behaviour 67:933-939.
—. 2005. Nepotistic mobbing behaviour in the Siberian jay, Perisoreus infaustus. Animal Behaviour 69:345-352.
Griesser, M., P. Halvarsson, S. M. Drobniak, and C. Vila. 2015. Fine-scale kin recognition in the absence of social cues in the Siberian jay, a monogamous bird species Molecular Ecology 24:5726-5738.
Griesser, M., P. Halvarsson, T. Sahlman, and J. Ekman. 2014. What are the strengths and limitations of direct and indirect assessment of dispersal? Insights from a long-term field study in a group-living bird species. Behavioral Ecology and Sociobiology 68:485-497.
Griesser, M., and S. Lagerberg. 2012. Long-term effects of forest management on territory occupancy and breeding success of an open-nesting boreal bird species, the Siberian jay. Forest Ecology and Management 271:58-64.
Griesser, M., and M. Nystrand. 2009. Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. Behavioral Ecology 20:709-715.
Griesser, M., M. Nystrand, S. Eggers, and J. Ekman. 2007. Impact of forestry practices on fitness correlates and population productivity in an open-nesting bird species. Conservation Biology 21:767-774.
—. 2008. Social constraints limit dispersal and settlement decisions in a group-living bird species. Behavioral Ecology 19:317-324.
Griesser, M., M. Nystrand, and J. Ekman. 2006. Reduced mortality selects for family cohesion in a social species. Proceedings of the Royal Society B-Biological Sciences 273:1881-1886.
Griesser, M., and T. N. Suzuki. 2016. Kinship modulates the attention of naïve individuals to the mobbing behaviour of role models. Animal Behaviour 112:83-91.
Griffin, A. S. 2004. Social learning about predators: A review and prospectus. Learning & Behavior 32:131-140.
Griffin, A. S., D. T. Blumstein, and C. S. Evans. 2000. Training Captive-Bred or Translocated Animals to Avoid Predators. Conservation biology 14:1317-1326.
Griffiths, R., M. C. Double, K. Orr, and R. J. G. Dawson. 1998. A DNA test to sex most birds. Molecular Ecology 7:1071-1075.
Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1-22.
Hollén, L. I., and A. N. Radford. 2009. The development of alarm call behaviour in mammals and birds. Animal Behaviour 78:791-800.
Hoppitt, W., and K. N. Laland. 2008. Social processes influencing learning in animals: a review of the evidence. Advances in the Study of Behavior 38:105-165.
Kenward, R. E. 1978. Hawks and Doves - Factors Affecting Success and Selection in Goshawk Attacks on Woodpigeons. Journal of Animal Ecology 47:449-460.
Li, D. 2002. Hatching responses of subsocial spitting spiders to predation risk. Proceedings of the Royal Society of London B: Biological Sciences 269:2155-2161.
Lönnstedt, O. M., M. I. McCormick, M. G. Meekan, M. C. Ferrari, and D. P. Chivers. 2012. Learn and live: predator experience and feeding history determines prey behaviour and survival. Proceedings of the Royal Society of London B: Biological Sciences:rspb20112516.

Magrath, R. D., T. M. Haff, J. R. McLachlan, and B. Igic. 2015. Wild birds learn to eavesdrop on heterospecific alarm calls. Current Biology 25:2047-2050.
Manassa, R., and M. McCormick. 2013. Social learning improves survivorship at a life-history transition. Oecologia 171:845-852.
Nystrand, M. 2006. Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays. Behavioral Ecology 17:503-509.
R Core Team. 2016.R: A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria. .
Reader, S. M., and D. Biro. 2010. Experimental identification of social learning in wild animals. Learning & Behavior 38:265-283.
Rendell, L., R. Boyd, D. Cownden, M. Enquist, K. Eriksson, M. W. Feldman, L. Fogarty et al. 2010. Why copy others? Insights from the social learning strategies tournament. Science 328:208-213.
Shier, D. M., and D. H. Owings. 2007. Effects of social learning on predator training and postrelease survival in juvenile black-tailed prairie dogs, Cynomys ludovicianus. Animal Behaviour 73:567-577.
Smith, H. J. 2009, Parenting for primates, Harvard University Press.
Storm, J. J., and S. L. Lima. 2010. Mothers forewarn offspring about predators: a transgenerational maternal effect on behavior. The American Naturalist 175:382-390.
Suzuki, T. N. 2016. Semantic communication in birds: evidence from field research over the past two decades. Ecological Research 31:307-319.
Svensson, L. 2006, Identification Guide to European Passerines. Thetford, British Trust for Ornithology.
van Schaik, C. P. 2010. Social learning and culture in animals, Pages 623-653 Animal behaviour: Evolution and mechanisms, Springer.
Wisenden, B. D. 2003. Chemically mediated strategies to counter predation, Pages 236-251 Sensory processing in aquatic environments, Springer.
Wisenden, B. D., and M. C. Millard. 2001. Aquatic flatworms use chemical cues from injured conspecifics to assess predation risk and to associate risk with novel cues. Animal Behaviour 62:761-766.

Table 1: **Effect of predator exposures during autumn on first winter survival (i) and the subsequent acquisition of a breeding position (ii) in Siberian jays.**

i) first winter survival

Factor	Posterior mean	Upper to lower CI	Effective sampling	*P* MCMC
intercept	1.15	0.75 to 1.58	1003	0.0009
goshawk seen: yes	**0.42**	**0.12 to 0.69**	**1094**	**0.009**
sparrowhawk seen: yes	0.23	-0.02 to 0.5	1094	0.091
Ural owl seen: yes	-0.15	-0.38 to 0.09	1094	0.203
hawk owl seen: yes	-0.09	-0.39 to 0.23	1094	0.543
kinship: unrelated immigrants	0.01	-0.15 to 0.17	1094	0.907
sex: male	0.09	-0.05 to 0.26	1094	0.282
group size	**-0.12**	**-0.22 to -0.04**	**1094**	**0.013**
habitat structure	0.06	-0.17 to 0.34	1094	0.651

ii) becoming a breeder

Factor	Posterior mean	Lower to upper CI	Effective sampling	*P* MCMC
intercept	0.15	-0.38 to 0.57	1094	0.559
goshawk seen: yes	**0.44**	**0.11 to 0.79**	**1094**	**0.015**
sparrowhawk seen: yes	**0.3**	**0.01 to 0.6**	**1094**	**0.048**
Ural owl seen: yes	-0.16	-0.45 to 0.12	1094	0.263
hawk owl seen: yes	-0.23	-0.57 to 0.11	1094	0.192
kinship: unrelated immigrants	0.14	-0.03 to 0.32	1094	0.108
sex: male	0.15	-0.05 to 0.31	1094	0.095
group size	-0.01	-0.12 to 0.09	1094	0.854
habitat structure	0.02	-0.26 to 0.29	1094	0.905

Juveniles observed breeders mobbing a goshawk only or as well a hawk owl ($N = 24$), a sparrowhawk only or as well an Ural owl ($N = 16$), a Ural owl or a hawk owl ($N = 13$), or had never been knowledgeable any predator exposure ($N = 56$). Data were analyzed using the MCMCglmm package (binomial distribution). Significant factors are highlighted in bold.

Figure legends:

Figure 1. **Timeline of the natural history of Siberian jays, the presence of natural predators at the study site and our experiments, as well as the subsequent observations to assess the survival and acquisition of breeding position.** GH = goshawk, O = owls, SH = sparrowhawk.

Figure 2. **Effect of predator exposures during autumn on first winter survival and the subsequent acquisition of a breeding position in Siberian jays.** Juveniles observed breeders mobbing a goshawk only or as well a hawk owl (N = 24), a sparrowhawk only or as well an Ural owl (N = 16), an Ural owl or hawk owl (N = 13), or had not been experimentally exposed to a predator (N = 56).

Figure 1:

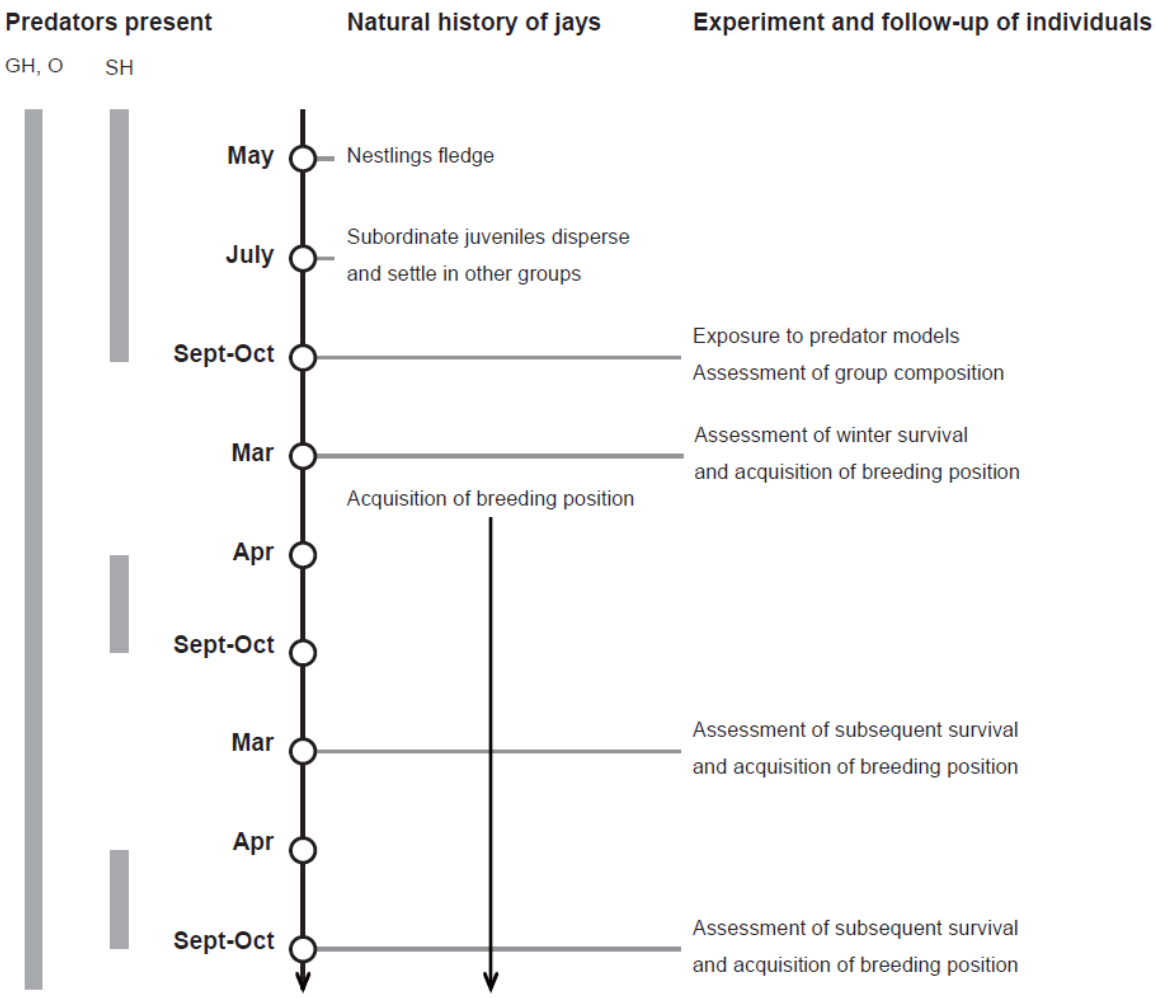
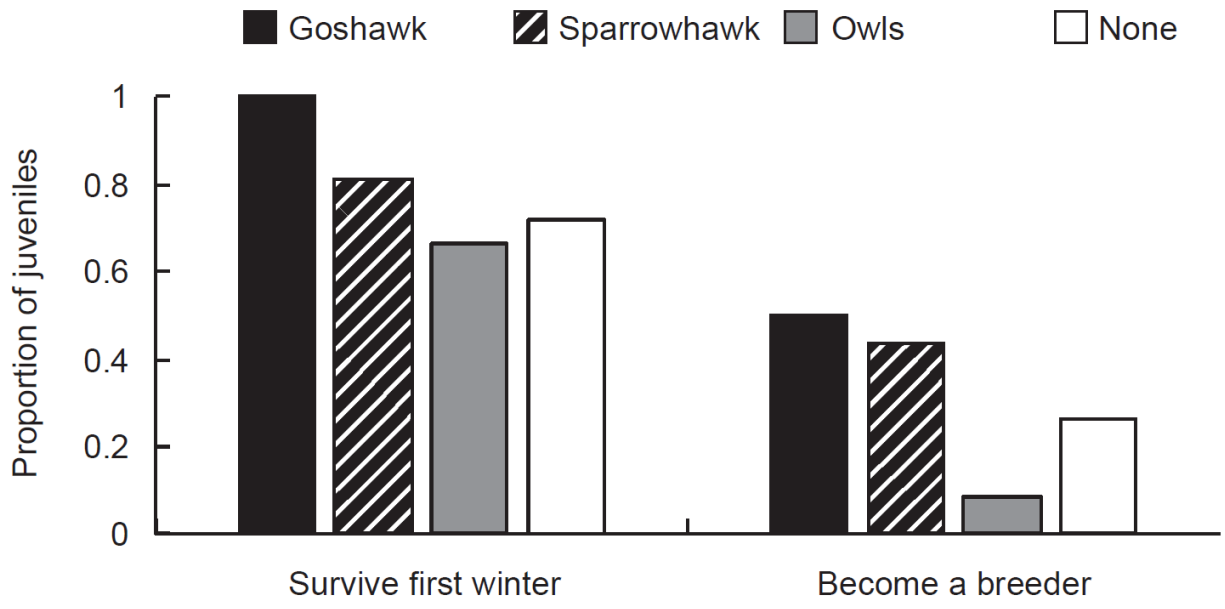

Predators present
GH, O
SH
Natural history of jays
Experiment and follow-up of individuals
May
Nestlings fledge
July
Subordinate juveniles disperse
and settle in other groups
Sept-Oct
Exposure to predator models
Assessment of group composition
Mar
Assessment of winter survival
and acquisition of breeding position
Acquisition of breeding position
Apr
Sept-Oct
Mar
Assessment of subsequent survival
and acquisition of breeding position
Apr
Sept-Oct
Assessment of subsequent survival
and acquisition of breeding position

Figure 2:


Goshawk
Sparrowhawk
Owls
None
Proportion of juveniles
1
0.8
0.6
0.4
0.2
0
Survive first winter
Become a breeder